Characteristics of the vertebrate-dispersed fruits of sixteen Northern Territory monsoon forest tree species

CHRISTINE S. BACH[1,2], DONALD C. FRANKLIN[3] AND GEORGE LAMBRINIDIS[1]

*[1]Faculty of Edncation, Health and Science, Charles Darwin University,
Darwin NT 0909, AUSTRALIA*

*[2]Current address: Dripstone High School, PO Box 41370
Casnarina NT 0811, AUSTRALIA*

*[3]School for Environmental Research, Charles Darwin University,
Darwin NT 0909, AUSTRALIA*

Corresponding anthor: don.franklin@cdu.edn.au

ABSTRACT

The monsoon forests of the Top End of the Northern Territory eontain an unusually high proportion of tree speeies with vertebrate-dispersed fruits, but the corresponding fauna is disproportionately speeies-poor. We doeument and compare the morphology, moisture content, nutrient eontent and crop size of sixteen eommon fleshy- or arillate-fruited tree species from the region. Arils were mueh rieher in lipids and lower in earbohydrates than fleshy fruits. A gradient of flesh nutrient eontents from high levels of carbohydrates to high levels of nutrients that are more eostly for the plant to produce was identified. Howevcr, this gradient was not related to other fruit eharaeters, providing only weak support for the generalist-speeialist paradigm in the evolution of vertebrate-dispersed fruits. Evidence was obtained of a trade-off between the size and number of fruits. Compared to other tropieal regions, the flesh of the speeies sampled was high in earbohydrates and low in eostly nutrients.

KEYWORDS: Top End, rainforest, dispersal, frugivory, nutrients, moisture content, fruit morphology, crop size, fleshy fruits, arillate fruits, birds, flying-fox.

INTRODUCTION

Fleshy fruits attraet animals – particularly vertebrates but also ants and some other invertebrates – in order to disperse their seeds (van der Pijl 1982). Fruits vary in colour, size, structure, nutritional eontent and abundance, thus attraeting different animal speeies, or the same speeies in different proportions and frequencies (Snow 1971; Willson and Whelan 1990; Wheelwright 1993; Sehaefer *et al.* 2003; Bollen *et al.* 2004; Lord 2004). The eonsequenees of this variation for dispersal, reproduetive success and the evolution of fruit eharaeters has reeeived much observational, experimental and theoretieal attention (e.g. MeKey 1975; Stapanian 1982; Fleming *et al.* 1993; Jordano 1995; Levey *et al.* 2002).

Fleshy fruits evolved with the development of environments in whieh germination sites are shady and spatially unpredietable – in short, the tropieal rainforest – where they are strongly associated with the diversifieation of woody plants (Bolmgren and Eriksson 2005). Within tropical forests, the proportion of trees that are vertebrate-dispersed is positively eorrelated with mean annual rainfall (Hartshorn 1983; Willson *et al.* 1989; Bullock 1995). It is perhaps surprising then, that 84% of 166 tree species in the mostly semi-deeiduous monsoon rainforests (hereafter,

monsoon forests) of the Top End of the Northern Territory have fleshy, arillate or other vertebrate-dispersed fruits (Table 1). This percentage is at the high end of the range for all tropical forests (Howe and Smallwood 1982), similar to that reported for the evcrgreen rainforests of north Queensland (Webb and Traeey 1981), and mueh higher than the comparable rate of 51% in a seasonally dry tropical forest in Costa Riea (Frankie *et al.* 1974).

This anomaly may be the produet of proeesses that favour vagility (Russell-Smith and Dunlop 1987). Monsoon forest patches in the Top End are small (Russcll-Smith 1991), sueh that tree populations may laek viability unless genetie diversity is maintained by dispersal among patehes (Russell-Smith and Lee 1992; Shapeott 1998, 1999). Furthermore, the region's monsoon forest estate has expanded from Pleistoeene refugia (Shapeott 2000), and many patehes are on reeent (Holocene) landforms (Russell-Smith and Dunlop 1987), a proeess demanding effeetive long-distanee dispersal.

However, this riehness amongst trees has no parallel amongst the frugivores able to provide dispersal serviees to them. There are at most eight obligate, non-destruetive frugivores in Top End monsoon forests, all of whieh are birds, and an additional six opportunistieally but

Table 1. Fruit types of the flowering plants of Top End monsoon forests and their assumed dispersal agents, summarised from Russell-Smith and Dunlop (1987). Presented fruits are dry, brightly coloured or glistening, and exposed when ripe so as to attract vertebrates; it corresponds to the mimetic endozoochore class of bird-dispersed plants as described by van der Pijl (1982).

| | % of species | | |
| | Trees | Other plants | Total |
Fruit type (dispersal agents)	n = 166 spp.	n = 161 spp.	n = 327 spp.
Fleshy (vertebrates)	65	48	57
Arillate or funiculate (vertebrates)	5	1	3
Presented (vertebrates)	14	3	9
Other (abiotic or non-vertebrate)	16	48	32

extensively frugivorous species (Table 2), a fauna that is depauperate compared to that in the tropical rainforests of north Queensland (Crome 1975) and Papua New Guinea (Brown and Hopkins 2002). The resultant ratio of one frugivore species for every ten tree species (14:140) is markedly less than the 1:3 ratio demonstrated for Neotropical forests (Fleming 2005).

With a depauperate frugivore fauna that is thus likely to contain fewer specialists, evolutionary generalisation of frugivore-fruit relationships and thus of fruit characters, in Top End monsoon forests might be anticipated. McKey (1975) proposed that a typical generalised fruit is produced in abundance, synchronously within individuals and populations, is small and/or has small and often multiple seeds, and is cheap to produce – having high levels of moisture and carbohydrates and low levels of expensive nutrients such as lipids and protein. Willson *et al.* (1989) noted that bird-dispersed fruits in the Australasian region are predominantly red or black but sometimes blue or yellow, whereas mammal-dispersed fruits are frequently brown, green, orange or yellow. It is also possible that the range of evolutionary options for variation in fruit traits is constrained by soil moisture and/or canopy type (Bullock 1995; Franklin and Bach 2006). There has, however, been no attempt to systematically describe the traits of vertebrate-dispersed fruits in Top End monsoon forests beyond the characterisation of Russell-Smith and Dunlop (1987) summarised here in Table 1.

In this study, we describe the morphology, moisture and nutrient contents of the fruit of sixteen common vertebrate-dispersed (zoochorous) trees from the monsoon forests of the Top End of the Northern Territory. The observed traits are then evaluated for evidence of gradients and associations which might correspond to generalised and specialised dispersal syndromes *sensu* McKey (1975). Some implications of our results for frugivory in the monsoon forests of the Northern Territory are briefly discussed.

Table 2. Vertebrates that are obligate frugivores or extensively frugivorous and occur in Top End monsoon forests. The Top End occurrence of species marked with an asterisk is primarily in monsoon forests; others, such as the mistletoebird (Woinarski *et al.* 1988), may be more abundant in nearby savannas. The non-volant species have limited home ranges and thus are most unlikely to provide inter-patch dispersal services. Many other vertebrates consume and may disperse fruits but are not specialists. Some monsoon forest rodents consume fleshy fruits but also consume the seeds and are thus seed predators rather than dispersal agents (Begg and Dunlop 1985; Firth *et al.* 2005). Additional sources: Morton and Brennan (1991), Woinarski (1993), Bowman and Woinarski (1994), Higgins (1999), Palmer *et al.* (2000), Price (2004).

Species	Family
More or less obligately frugivorous, volant	
* Emerald dove *Chalcophaps indica*	Columbidae
* Banded fruit-dove *Ptilinopus cinctus*	Columbidae
* Rose-crowned fruit-dove *P. regina*	Columbidae
* Pied imperial-pigeon *Ducula bicolor*	Columbidae
* Common koel *Eudynamys scolopacca*	Cuculidae
* Channel-billed cuckoo *Scythrops novaehollandiae*	Cuculidae
* Figbird *Sphecotheres viridis*	Oriolidae
Mistletoebird *Dicaeum hirundinaceum*	Dicaeidae
Opportunistically but extensively frugivorous, volant	
* Yellow oriole *Oriolus flavocinctus*	Oriolidae
* Varied triller *Lalage leucomela*	Campephagidae
Great bowerbird *Chlamydera nuchalis*	Ptilonorhynchidae
Black flying-fox *Pteropus alecto*	Pteropodidae
Opportunistically but extensively frugivorous, non-volant	
* Black-footed tree-rat *Mesembriomys gouldi*	Muridae
Common brush-tailed possum *Trichosurus vulpecula*	Phalangeridae

METHODS

Study area and species. Fruit samples and crop size data were collected from monsoon forests on Gunn Point Peninsula (12°24'S, 131°02'E), 40 km north-east of Darwin, Northern Territory. Mean annual rainfall is *c.* 1700 mm, with 97% falling in the wet season months of October to April. Temperatures are warm to hot throughout the year, with diurnal variation mostly less than 12°C and night-time temperatures rarely if ever dropping below 10°C.

On Gunn Point Peninsula as elsewhere in the Top End of the Northern Territory, monsoon forests occur as isolated and mostly tiny patches embedded within a dominant savanna matrix (Russell-Smith 1991). In the study area, they occur in two discrete landscape settings, on clay-loams around springs at the edge of floodplains, and on seasonally dry coastal cheniers (coral sands or sandy-loams). In the former setting, most trees are evergreen; in the latter, deciduousness is prominent (Bach 2002). Whilst there is some floristic overlap between settings, the contrast corresponds with the primary floristic

division within Top End monsoon forests (Russell-Smith 1991), with spring-fed sites belonging to Russell-Smith's Group 2 and the coastal chenier sites to Group 9.

Sixteen tree species were selected for study (Table 3), eight from the spring-fed patches and eight from seasonally dry sites, though species associated with one forest type may occur in the other type elsewhere. They were selected on the basis that: *a,* they were common in their respective forest type in the study area; *b,* their fruits are an important food resource for frugivorous birds and flying-foxes (Price 1998, Palmer *et al.* 2000); and *c,* no two species were from the same family, thus providing phylogenetic independence of fruit traits.

Analysis has been conducted using the units dispersed by vertebrates. In most species, this corresponds to the fruit. In *Cupaniopsis anacardioides* and *Myristica insipida,* the fruit is woody, splitting to reveal the arillate seed(s), and the dispersal unit is taken to be the seed plus its associated aril. *Cupaniopsis anacardioides* has three small seeds per fruit and thus three dispersal units per fruit, whereas *M. insipida* fruits contain a single large seed. The other exception is *Strychnos lucida,* in which the seeds are embedded in a semi-liquid pulp (mesocarp) which is surrounded by a thin but firm shell (exocarp). Observations indicate that birds normally break the shell and consume the contents, and damaged empty shells commonly remain on the tree. For *S. lucida,* the dimensions (length, width) are for the entire fruit, but mass, moisture content and nutrient analyses are for the contents only.

Fruit abundance. In the course of phenological studies (Bach 2002; Franklin and Bach 2006), fruit abundance was estimated monthly over 30 months for each of between eight and sixteen marked, mature individuals

of each species (females in dioecious species). Estimates were visual, aided with binoculars where necessary, and categoric, estimates being in classes of 0, 1–10, 11–50, 51–100, 101–500, 501–1000, … 1000001–5000000. No distinction is made between unripe and ripe fruit because ripe fruit were rarely seen in the majority of species.

Fruit collection. Fresh, ripe fruit showing no sign of damage or desiccation were collected directly from three to five plants of each species (74 plants in total). In the case of the tall tree *Gmelina schlechteri,* fruit were collected from the ground. Collected fruits were kept cool until returned to the laboratory.

Morphological and nutrient analyses. In the laboratory, the samples were divided into two subsets: *a,* a random sample of 60 dispersal units per species for determination of morphological characters and moisture content; and *b,* a set of 6 to 10 dispersal units per species, two per tree, for nutrient analysis of the flesh. In the case of *Ficus virens,* the seeds are numerous and minute, and could not be separated from the flesh, so they were included in the nutrient analysis.

For each dispersal unit in subset *a,* length, width, number of seeds (*F. virens* excepted) and fresh mass of seeds and flesh were determined. *Per capita* dry mass and water content of flesh and seed were determined after freeze-drying. Length and width were measured to 0.01 cm. Where the fruit was the dispersal unit, the length was taken as the distance from the pedicel junction to the apex, and the width as the widest point perpendicular to the length; thus, in some cases width may be longer than length. Mass was determined on an electronic balance with a precision of 0.001 g.

Table 3. Classification and *a priori* characteristics of 16 species of monsoon forest trees from northern Australia. Canopy types are from Franklin and Bach (2006).

Species	Family	Fruit type	Fruit colour	Canopy type
Canarium australianum F.Muell.	Burseraceae	drupe	blue-purple	deciduous
Carallia brachiata (Lour.) Merr.	Rhizophoraceae	berry	red	evergreen
Carpentaria acuminata (H.Wendl. and Drude) Becc.	Arecaceae	berry	red	evergreen
Cupaniopsis anacardioides (A.Rich) Radlk.	Sapindaceae	arillate	orange-red	evergreen
Diospyros compacta (R.Br.) Kosterm.	Ebenaceae	berry	red	evergreen
Drypetes deplanchei (Brongn. and Griseb.) Merr.	Euphorbiaceae	drupe	orange-red	evergreen
Elaeocarpus arnhemicus F.Muell.	Elaeocarpaceae	drupe	blue	partly deciduous
Ficus virens Aiton	Moraceae	fig	white-purple	partly deciduous
Gmelina schlechteri H.J.Lam	Verbenaceae	drupe	red-purple	partly deciduous
Maranthes corymbosa Blume		drupe	purple	evergreen
Miliusa brahei (F. Muell.) Jessup	Annonaceae	berry	purple-black	deciduous
Mimusops elengi L.	Sapotaceae	berry	orange-red	evergreen
Myristica insipida R.Br.	Myristicaceae	arillate	red	evergreen
Strychnos lucida R.Br.	Loganiaceae	berry	yellow-orange	partly deciduous
Syzygium nervosum DC.	Myrtaceae	berry	purple-black	evergreen
Terminalia microcarpa Decne.	Combretaceae	drupe	blue-purple	partly deciduous

Flesh from the second subset was removed and pooled into replicate samples (trees), freeze-dried, ground and stored in sealed vials at -80°C prior to analysis. Ash content was determined gravimetrically after heating weighed samples (approximately 1 g) at 500°C in a muffle furnace overnight. To determine soluble carbohydrate content, samples of $c.$ 0.006 g were analysed spectrophotometrically using the phenol-sulphuric acid method of Dubois *et al.* (1956). Total lipid content was determined gravimetrically after extraction from samples of $c.$ 0.1 g with chloroform-methanol (2:1) (Bligh and Dyer 1959). Total Kjeldahl Nitrogen content was determined using samples of $c.$ 0.1 g digested in sulphuric acid. Since high lipid contents can interfere with the nitrogen analysis (Oomah and Bushuk 1983), samples were defatted before analysing for nitrogen (residues of the lipid extraction stored on filter paper). The digested samples were then analysed using a flow injection analyser (Lachat Instruments QuikChem method 13-107-06-2-D).

To assess the efficiency of each method, trials were conducted in which known amounts of glucose (a soluble carbohydrate), stearic acid (a lipid) and glycine (a protein) were processed as for the flesh samples. Recovery rates (mean ± s.d.) were: glucose – 99.2 ± 7.5 % (n = 14); stearic acid – 102.91 ± 3.31 % (n = 12); and glycine – 100.032 ± 4.319 % (n = 10). As these rates were considered sufficiently accurate, no adjustment was made to the analytical results.

Data analysis. Our index of maximum crop size for each species is the median of the maximum fruit abundance recorded for individuals of that species over the thirty months of recording. As crop size varied hugely among species (our index ranges over 2.5 orders of magnitude, Table 4), this method was considered to be of sufficient accuracy for correlative purposes.

Flesh/dispersal unit mass was estimated using fresh weights. Crude protein content was estimated by multiplying Total Kjeldahl Nitrogen content by 6.25.

For the 14 non-arillate species, the correlation matrix for eight fruit characters (dispersal unit mass, flesh/dispersal unit mass, flesh moisture content, % dry mass of ash, soluble CHO, lipids and protein, and maximum crop size) were examined using Principal Components Analysis (PCA) implemented in Statistica (StatSoft 1984–2004). As maximum crop size was not normally distributed, data were converted to an index based on the observation classes (see Methods) in which the smallest observed median maximum crop size class (51–100) was scored as one, the next possible class as two and so on, the largest observed class (10,001–50,000) receiving a score of eight. For *F. virens*, flesh was taken to comprise 100% of the dispersal unit mass.

RESULTS

The fruits of seven species (44%) were berries, six (38%) were drupes, two (13%) were arillate and one was a fig (Table 3). The ripe fruits of eight species (50%) including the arils of the two arillate species were red, orange-red or yellow-orange and six (38%) were blue, purple, blue-purple or purple-black, the remaining two species being white-purple and red-purple (Table 3). Dispersal units ranged in mass (size) from the 0.29 g (0.7 x 0.8 cm) berry of *Carallia brachiata* to the 4.46 g (2.7 x 1.6 cm) drupe of *Maranthes corymbosa* (Table 4). Most dispersal units were single-seeded, with a maximum of 3.1 seeds per unit in the berry of *Diospyros compacta* (Table 4).

The arils of *Cupaniopsis anacardioides* and *Myristica insipida* had lower moisture and carbohydrate content, and higher lipid and protein content, than the flesh of any non-arillate species (Table 4). This was markedly so for lipid content, which was 4.2 and 6.1 times higher respectively than the most lipid-rich non-arillate species (*Canarium australianum*). Amongst non-arillate species, flesh varied from 53–81% of dispersal unit (fresh) mass and flesh moisture content from 60–96% by mass (Table 4). The nutrient content (dry mass) of the flesh of non-arillate species varied from 27–70% soluble carbohydrate, 3–9% ash, 2–12% lipids and 2–7% protein (Table 4).

Principal Components Analysis of non-arillate species demonstrated an association of high levels of protein, lipids and ash with low levels of soluble carbohydrates (CHO) (Fig. 1; gradient approx. parallel to Factor 1). A second association existed between larger dispersal unit mass and smaller crop size. In the first two factors of the PCA, the moisture content of flesh was unrelated to any other fruit character.
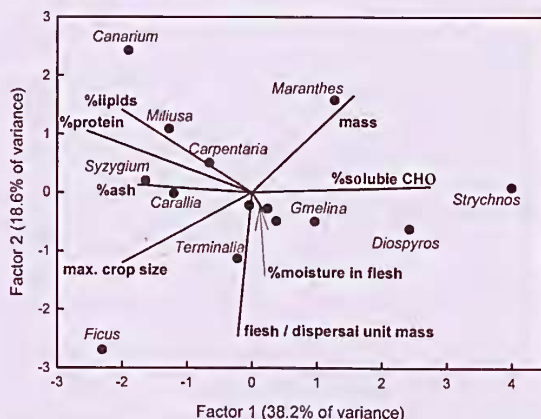

Fig. 1. The first two factors of a Principal Components Analysis of fruit characters of 14 non-arillate monsoon forest tree species. Fruit characters (lines, labelled in bold) are as in Table 4; their factor scores have been multiplied by three for clarity. Not all tree species are labelled; species are spelt out in full in Table 3.

DISCUSSION

Associations and gradients amongst fruit traits.
Our demonstration of a nutrient gradient in the flesh of
fruits from high concentrations of proteins, lipids and ash
to high concentrations of soluble carbohydrates is similar
to the primary gradient identified by Herrera (1987) in an
analysis of 111 temperate-zone plants. Although excluded
from our gradient analysis, the arillate species serve
to reinforce this primacy, both arillate species having
exceptionally high levels of lipids and protein and low
levels of soluble carbohydrates. In that lipids, protein and
ash are expensive nutrients whereas soluble carbohydrates
are cheap to produce, this gradient represents a spectrum
of dispersal syndromes ranging from specialised to
generalised (McKey 1975).

However, other traits thought to represent extremes
of adaptive specialisation and generalisation in dispersal
syndromes (McKey 1975) were not consistently associated
with the primary gradient we identified. We found
evidence of a trade-off between crop size (measured as
the number of fruits) and individual fruit mass, but this
was not related to the nutrient gradient. There was no
relationship between the primary gradient and relative
commitment to flesh or seed. Multiple seeds, a feature
associated with generalised dispersal syndromes, were
a feature of two species with high content of soluble
carbohydrates (*Diospyros compacta, Strychnos lucida*) but
also of two species towards the other end of the primary
gradient (*Ficus virens, Miliusa brahei*). Franklin and Bach
(2006) identified *Carpentaria acuminata* and *F. virens*
as fruiting asynchronously among individuals, a feature
associated with dispersal specialisation, and both species
had 'specialised' fruit nutrients, i.e. low to moderate levels
of soluble CHO and high concentrations of one or more of
ash, lipids or protein. However, the generalist-specialist
paradigm predicts that asynchronous fruiting will be
associated with small maximum crop sizes, whereas *F.
virens* had the largest crop size and *C. acuminata* the equal
second largest crop size in this study. In Herrera's (1987)
study, protein and ash contents were positively correlated
but protein and lipid content were not. Furthermore, and
in converse to predictions arising from the generalised-
specialised paradigm, Herrera (1987) found that fruit size
was negatively correlated with lipid content (and thus was
positively correlated with soluble carbohydrate content),
whilst flesh / dispersal unit mass was negatively correlated
with protein content.

Exceptionally high levels of lipids and protein and
correspondingly low levels of moisture and soluble
carbohydrates may be a general feature of the arils of
vertebrate-dispersed fruit (Howe and Vande Kerckhove
1981; Foster and McDiarmid 1983; Pizo and Oliveira
2001). The arillate *Myristica insipida* of this study exhibits
additional traits which may be regarded as specialised
(*cf* McKey 1975). These include small crop size, a fairly

large dispersal unit with a particularly large seed, and
fruiting phenology. Though flowering by female plants
(the species is dioecious) is seasonal (Armstrong and
Irvine 1989, Franklin and Bach 2006), *M. insipida* fruits
throughout the year (Franklin and Bach 2006) with
progressive ripening of a few fruit at a time (C.S. Bach
pers. obs.). Furthermore, and notwithstanding small crop
sizes, energetic allocation to fruit production in *M. insipida*
far outweighs commitment to flowering (Armstrong and
Irvine 1989).

It is possible, therefore, to identify species that are
particularly consistent with the generalist-specialist
paradigm for the evolution of fruit characters, but also
many that are not. This paradigm currently receives
at most only highly qualified acceptance (Howe 1993;
Levey *et al.* 2002). Exceptions may arise, or the paradigm
fail completely, for a variety of reasons including that
selection on fruit characteristics for dispersal is limited
by phylogenetic and abiotic constraints (Herrera 1992,
1998; Hampe 2003), that dispersal success may often
be irrelevant to plant demographics (Howe and Miriti
2004), that the relationship between fruit and frugivores
may be in disequilibrium (Levey and Benkman 1999)
or strongly asymmetric (Bascompte *et al.* 2006), or that
attraction of a variety of dispersal agents may lead to
differing and even opposing selection pressures (Russo
2003). Furthermore, the examination of co-evolution in
plants and their vertebrate dispersers is confounded by
often complex scale-dependence (Russo 2003; Burns
2004; Garcia and Ortiz-Pulido 2004). Rather than reject
the paradigm, we prefer the interpretation that it is but one
of many effects influencing a complex mutualistic system,
many of which do not directly relate to the behaviour of
vertebrate dispersal agents. In his much more extensive
study, Herrera (1987) drew similar conclusions, noting
in particular the roles of phylogeny, constraints to fruit
architecture, and species-specific energy and nutrient
allocation patterns in influencing fruit traits.

Some implications for frugivory. We sampled only
a small proportion of tree species in Top End monsoon
forests – c. 14% of fleshy-fruited species and 25% of
arillate species – and in selecting common species our
study may be biased towards generalists. Thus it is not
possible for us to appraise the hypothesis that Top End
monsoon forests have been filtered to favour generalised
dispersal syndromes, or that species have evolved in that
direction. The species we selected were, compared to a
range of tropical environments as summarised by French
(1991; Table 6), of typical mass (1.64 *cf* 1.76 g), flesh /
dispersal unit wet mass (60.5 *cf* 57.4%) and % moisture
in flesh (76 *cf* 72%) (data are means of species means).
However, mean levels of soluble CHO were higher (42 *cf*
31%), and levels of lipids (12 *cf* 21%) and protein (5.3 *cf*
8.8%, estimated using the same conversion from %
nitrogen as applied to our data) lower than in other regions,
suggesting either that our sample, or Top End monsoon

Table 4. Dimensions, moisture content and nutrient content of the dispersal units of 16 species of monsoon forest trees from northern Australia. Data are means ± standard error. For dimensions and moisture content, n = 60 for each species. For nutrient analyses, n = 10 per species (2 per tree x 5 trees) except *E. arnhemicus*, *C. acuminata* and *S. nervosum*, for which n = 6 per species (2 per tree x 3 trees). Maximum crop size is the median of the maximum observed for each individual of the species. Flesh (% mass) is flesh / dispersal unit (fresh) mass x 100. Bracketed measurements for *F. virens* are for the flesh combined with the numerous tiny seeds. Bracketed means indicate that *Ficus virens* has been excluded.

Species	Length (cm)	Width (cm)	Mass (g)	Seeds per unit	Maximum crop size	Flesh (% mass)	Moisture (% mass) Flesh	Moisture (% mass) Seed	Nutrient content of flesh (% dry mass) Ash	Nutrient content of flesh (% dry mass) Lipids	Nutrient content of flesh (% dry mass) Protein	Nutrient content of flesh (% dry mass) Soluble CHO
Arillate species												
Cupaniopsis anacardioides	1.2 ± 0.02	0.7 ± 0.01	0.38 ± 0.010	1 ± 0	300	29.6 ± 0.61	52.3 ± 0.80	19.9 ± 0.90	3.6 ± 0.16	51.6 ± 2.64	9.3 ± 0.55	23.1 ± 1.71
Myristica insipida	2.0 ± 0.02	1.2 ± 0.01	1.77 ± 0.035	1 ± 0	75	18.1 ± 0.60	35.1 ± 0.49	46.5 ± 1.65	1.2 ± 0.09	75.2 ± 0.60	5.7 ± 0.18	9.2 ± 0.59
Non-arillate species												
Canarium australianum	2.2 ± 0.04	1.3 ± 0.01	2.62 ± 0.078	1 ± 0	750	56.3 ± 0.28	62.5 ± 0.27	17.6 ± 0.19	5.6 ± 0.17	12.4 ± 1.13	7.2 ± 0.35	35.5 ± 1.25
Carallia brachiata	0.7 ± 0.01	0.8 ± 0.01	0.29 ± 0.006	1 ± 0	750	70.1 ± 0.43	96.4 ± 0.29	55.1 ± 0.46	5.4 ± 0.22	9.1 ± 0.64	5.9 ± 0.19	41.8 ± 1.23
Carpentaria acuminata	1.7 ± 0.01	1.7 ± 0.02	3.28 ± 0.078	1 ± 0	3000	62.1 ± 0.41	92.1 ± 0.18	38.7 ± 0.45	9.4 ± 0.19	2.8 ± 0.15	5.7 ± 0.17	42.7 ± 0.88
Diospyros compacta	1.1 ± 0.01	1.3 ± 0.01	1.49 ± 0.040	3.1 ± 0.17	300	67.6 ± 1.22	76.2 ± 0.38	37.9 ± 0.86	3.2 ± 0.18	1.6 ± 0.19	2.4 ± 0.06	57.8 ± 0.84
Drypetes deplanchei	1.3 ± 0.01	0.9 ± 0.01	0.70 ± 0.012	1 ± 0	300	68.9 ± 0.73	76.3 ± 0.37	28.0 ± 0.16	6.7 ± 0.17	3.1 ± 0.19	5.1 ± 0.16	44.1 ± 1.20
Elaeocarpus arnhemicus	1.4 ± 0.01	1.0 ± 0.01	0.95 ± 0.014	1 ± 0	3000	59.2 ± 0.77	68.1 ± 0.39	26.7 ± 0.26	2.9 ± 0.27	4.0 ± 0.33	3.7 ± 0.09	40.4 ± 1.45
Ficus virens	1.0 ± 0.01	1.0 ± 0.02	0.54 ± 0.025	many	30000		(77.2 ± 0.45)		(6.7 ± 0.41)	(6.1 ± 0.59)	(5.1 ± 0.18)	(31.0 ± 2.11)
Gmelina schlechteri	1.9 ± 0.03	1.4 ± 0.01	2.32 ± 0.063	1 ± 0	300	81.0 ± 0.26	89.7 ± 0.25	30.9 ± 0.34	4.2 ± 0.24	2.2 ± 0.14	5.6 ± 0.12	50.5 ± 1.04
Maranthes corymbosa	2.7 ± 0.03	1.6 ± 0.02	4.46 ± 0.178	1 ± 0	750	53.2 ± 1.25	84.5 ± 1.45	42.7 ± 0.37	5.0 ± 0.24	3.9 ± 0.09	4.7 ± 0.22	52.2 ± 0.72
Miliusa brahei	1.3 ± 0.02	1.4 ± 0.02	1.39 ± 0.050	1.4 ± 0.07	300	66.4 ± 0.55	83.2 ± 0.18	39.8 ± 0.24	8.8 ± 0.43	9.4 ± 0.46	6.3 ± 0.22	45.0 ± 1.23
Mimusops elengi	1.3 ± 0.01	1.2 ± 0.01	1.00 ± 0.020	1 ± 0	300	75.4 ± 0.45	60.4 ± 0.27	35.6 ± 0.25	5.0 ± 0.14	2.1 ± 0.13	5.1 ± 0.14	44.9 ± 1.73
Strychnos lucida	2.0 ± 0.04	2.0 ± 0.04	3.93 ± 0.260	2.1 ± 0.15	75	72.0 ± 0.62	85.4 ± 0.37	29.3 ± 0.43	3.3 ± 0.33	2.0 ± 0.18	1.8 ± 0.16	70.3 ± 3.02
Syzygium nervosum	0.9 ± 0.01	1.0 ± 0.01	0.57 ± 0.013	1 ± 0	3000	55.8 ± 1.01	83.6 ± 0.21	51.1 ± 0.61	5.4 ± 0.10	4.9 ± 0.19	5.9 ± 0.17	27.2 ± 0.49
Terminalia microcarpa	1.2 ± 0.01	0.9 ± 0.02	0.63 ± 0.022	1 ± 0	3000	71.6 ± 0.49	92.3 ± 0.20	33.3 ± 0.54	8.1 ± 0.50	2.5 ± 0.39	4.7 ± 0.18	52.5 ± 1.19
Mean of species means												
Arillate species	1.6	1.0	1.08	1		23.9	43.7	33.2	2.4	63.4	7.5	16.2
Non-arillate species	1.5	1.3	1.73	(1.3)		66.1	(80.8)	(35.9)	5.7	4.7	4.9	45.4
All species	1.5	1.2	1.64	1.2		(60.5)	(76.0)	(35.5)	5.3	12.0	5.3	41.8

forests in general, feature nutritionally cheap fruits. Based on colour, the species we selected are all consistent with a bird-dispersal syndrome (see particularly Willson *et al.* 1989) and, while there is some colour overlap with other dispersal syndromes, notably mammals, no colours specifically associated with a mammal dispersal syndrome – green and brown – were documented. This does not mean that no species was adapted to dispersal by mammals, but could mean that some species were adapted to dispersal by both birds and mammals.

There are no obligately frugivorous mammals in the Top End of the Northern Territory, and the extensively frugivorous mammal that is also flighted and thus offers potential for dispersal among isolated patches (Palmer and Woinarski 1999) is the black flying-fox, *Pteropus alecto* (Table 2). There is no quantitative data on the diet of the black flying-fox in the Top End, but Palmer *et al.* (2000) provided a list of 14 species of fruit consumed which includes seven of the species included in this study. All seven are also consumed by birds (Price 1998) (as are all the remaining species with the possible exception of *D. compacta*). Van der Pijl (1982) noted a range of characters associated with dispersal by bats, including exposed position such as cauliflory (fruits on the trunk), nocturnal and often musty, sour or rancid odour, drab colour and large size. Other than colour and size, these are not characters assessed here. We note that several monsoon forest tree species in the region are cauliflorous including palms (by structural definition) and several figs (*Ficus hispida, F. racemosa*). Fruit of the rotten cheesefruit, *Morinda citrifolia*, a widespread species of coastal and sub-coastal monsoon forests in the Top End (Liddle *et al.* 1994) are large, odorous and greenish-white, and may thus be particularly adapted to dispersal by bats.

The apparently specialised dispersal syndrome of arillate fruits demonstrated here and in other studies is consistent with a number of studies suggesting that arillate fruits attract a relatively narrow and specialised suite of vertebrates (Howe and Vande Kerekhove 1981; Foster and McDiarmid 1983; Brown and Hopkins 2002). Seventy-six percent of 70 feeding observations at *M. insipida* fruits in the Top End of the Northern Territory were of a single species, the obligately frugivorous rose-crowned fruit-dove, *Ptilinopus regina* (Price 1998). In Papua New Guinea, Brown and Hopkins (2002) found a positive association between birds of paradise and arillate fruits.

An alternate perspective on plant dispersal strategies is that fruit flesh could provide an attractive dry-season moisture resource for frugivores (Herrera 1982; Prinzinger and Schleucher 1998). This hypothesis leads to the prediction that species that fruit in the dry season, and especially species from dry monsoon forests where free water may be scarce at that time, should contain high moisture levels. Of the two species in this study whose fruit ripen in the dry season (Franklin and Bach 2006), one – *Mimusops elengi* – had exceptionally low moisture

levels. However, the second – *S. lucida* – features a semi-liquid pulp encased in an impervious shell which could well function as a source of moisture for frugivores.

In the Top End of the Northern Territory, the diet of only two vertebrate frugivores has been studied (Healey 1992; Palmer *et al.* 2000), and studies of avian frugivory are notably scant. Price *et al.* (1999), Price (2004) and Bach and Price (2005) provided alternative perspectives on the relationship between frugivores and their food resources. However, studies conducted from a plant ecological perspective, including patterns of fruit consumption, are needed to shed light on the adaptive and evolutionary processes at work on the Top End flora including the impact of a depauperate fauna on the rich assemblage of vertebrate-dispersed trees. No such autecological studies currently exist.

REFERENCES

Armstrong, J.E. and Irvine, A.K. 1989. Flowering, sex ratios, pollen-ovule ratios, fruit set and reproductive effort of a dioecious tree, *Myristica insipida* (Myristicaceae), in two different rain forest communities. *American Journal of Botany* 76: 74–85.

Bach, C.S. 2002. Phenological patterns in monsoon rainforests in the Northern Territory, Australia. *Austral Ecology* 27: 477–489.

Bach, C. and Price, O. 2005. Fruit resources, frugivore movements and landscape scale conservation in monsoon rainforests of northern Australia. Pp. 94–107. In: Gorman, J., Petheram, L. and Vigilante, T. (eds) *Old ways, new ways; wildlife management in northern Australia*. Charles Darwin University Press: Darwin.

Bascompte, J., Jordano, P. and Olesen, J.M. 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* 312: 431–433.

Begg, R.J. and Dunlop, C.J. 1985. The diets of the large rock-rat, *Zyzomys woodwardi*, and the common rock-rat, *Z. argurus* (Rodentia: Muridae). *Australian Wildlife Research* 12: 19–24.

Bligh, E.G. and Dyer, W.J. 1959. A rapid method of total lipid extraction and purification. *Canadian Journal of Biochemistry and Physiology* 37: 911–917.

Bollen, A., van Elsacker, L. and Ganzhorn, J.U. 2004. Relations between fruits and disperser assemblages in a Malagasy littoral forest: a community-level approach. *Journal of Tropical Ecology* 20: 599–612.

Bolmgren, K. and Eriksson, O. 2005. Fleshy fruits – origins, niche shifts, and diversification. *Oikos* 109: 255–272.

Bowman, D.M.J.S. and Woinarski, J.C.Z. 1994. Biogeography of Australian monsoon rainforest mammals: implications for the conservation of rainforest mammals. *Pacific Conservation Biology* 1: 98–106.

Brown, E.D. and Hopkins, M.J.G. 2002. Tests of disperser specificity between frugivorous birds and rainforest fruits in New Guinea. *Emu* 102: 137–146.

Bullock, S.H. 1995. Plant reproduction in neotropical dry forests. Pp. 277–303. In: Bullock, S.H., Mooney, H.A. and Medina, E. (eds) *Seasonally dry tropical forests*. Cambridge University Press: Cambridge.

Burns, K.C. 2004. Scale and macroecological patterns in seed dispersal mutualisms. *Global Ecology and Biogeography* 13: 289–293.

Crome, F.H.J. 1975. The ecology of fruit pigeons in tropical northern Queensland. *Australian Wildlife Research* 2: 155–185.

Dubois, M., Gilles, K.A., Hamilton, J.K., Rebers, P.A. and Smith, F. 1956. Calorimetric method for determination of sugars and related substances. *Analytical Chemistry* 28: 350–356.

Firth, R.S.C., Jefferys, E., Woinarski, J.C.Z. and Noske, R.A. 2005. The diet of the brush-tailed rabbit-rat (*Conilurus penicillatus*) from the monsoonal tropics of the Northern Territory, Australia. *Wildlife Research* 32: 517–523.

Fleming, T.H. 2005. The relationship between species richness of vertebrate mutualists and their food plants in tropical and subtropical communities differs among hemispheres. *Oikos* 111: 556–562.

Fleming, T.H., Venable, D.L. and Herrera, L.G. 1993. Opportunism vs. specialization: the evolution of dispersal strategies in fleshy-fruited plants. *Vegetatio* 107/108: 107–120.

Foster, M.S., McDiarmid, R.W. 1983. Nutritional value of the aril of *Trichilia cuneata*, a bird-dispersed fruit. *Biotropica* 15: 26–31.

Frankie, G.W., Baker, H.G. and Opler, P.A. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal af Ecology* 62: 881–913.

Franklin, D.C. and Bach, C.S. 2006. Assessing intraspecific phenological synchrony in zoochorous trees from the monsoon forests of northern Australia. *Journal of Tropical Ecology* 22: 419–429.

French, K. 1991. Characteristics and abundance of vertebrate-dispersed fruits in temperate wet sclerophyll forest in southeastern Australia. *Australian Journal of Ecology* 16: 1–13.

Garcia, D. and Ortiz-Pulido, R. 2004. Patterns of resource tracking by avian frugivores at multiple spatial scales: two case studies on discordance among scales. *Ecography* 27: 187–196.

Hampe, A. 2003. Large-scale geographical trends in fruit traits of vertebrate-dispersed temperate plants. *Journal of Biogeography* 30: 487–496.

Hartshorn, G.S. 1983. Plants. Introduction. Pp. 118–157. In: Janzen, D.H. (ed.) *Costa Rican natural history*. University of Chicago Press: Chicago.

Healey, C. 1992. Abundance, diet and roosting defecations of the Torresian imperial pigeon *Ducula spilorrhoa* in Darwin. *Corella* 16: 107–110.

Herrera, C.M. 1982. Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian dispersers. *Ecology* 63: 773–785.

Herrera, C.M. 1987. Vertebrate-dispersed plants of the Iberian Peninsula: A study of fruit characteristics. *Ecological Monographs* 57: 305–331.

Herrera, C.M. 1992. Interspecific variation in fruit shape: allometry, phylogeny, and adaptation to dispersal agents. *Ecology* 73: 1832–1841.

Herrera, C.M. 1998. Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: A 12-year study. *Ecological Monographs* 68: 511–538.

Higgins, P.J. (ed.) 1999. *Handbook of Australian, New Zealand & Antarctic Birds. Volume 4. Parrots to Dollarbird*. Oxford University Press: Melbourne.

Howe, H.F. 1993. Specialized and generalized dispersal systems: where does 'the paradigm' stand? *Vegetatio* 107/108: 3–13.

Howe, H.F. and Miriti, M.N. 2004. When seed dispersal matters. *BioScience* 54: 651–660.

Howe, H.F. and Smallwood, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201–228.

Howe, H.F., Vande Kerckhove, G.A. 1981. Removal of wild nutmeg (*Virola surinamensis*) crops by birds. *Ecology* 62: 1093–1106.

Jordano, P. 1995. Angiosperm fleshy fruits and seed dispersers: A comparative analysis of adaptation and constraints in plant-animal interactions. *American Naturalist* 145: 163–191.

Levey, D.J. and Benkman, C.W. 1999. Fruit-seed disperser interactions: timely insights from a long-term perspective. *Trends in Ecology & Evolution* 14: 41–43.

Levey, D.L., Silva, W.R. and Galetti M. (eds) 2002. *Seed dispersal and frugivory: ecology, evolution and conservation*. CAB International: Wallingford, UK.

Liddle, D.T., Russell-Smith, J., Brock, J., Leach, G.J. and Connors, G.T. 1994. *Atlas of the Vascular Rainforest Plants of the Northern Territory*. Australian Biological Resources Study: Canberra.

Lord, J.M. 2004. Frugivore gape size and the evolution of fruit size and shape in southern hemisphere floras. *Austral Ecology* 29: 430–436.

McKey, D. 1975. The ecology of coevolved seed dispersal systems. Pp. 159–191. In: Gilbert, L.E. and Raven, P.H. (eds) *Coevolution of animals and plants*. University of Texas Press: Austin.

Morton, S.R. and Brennan, K.G. 1991. Birds. Pp. 133–149. In: Haynes, C.D., Ridpath, M.G. and Williams, M.A.J. (eds) *Monsoonal Australia. Landscape, ecology and man in the northern lowlands*. A.A. Balkema: Rotterdam.

Oomah, B.D. and Bushuk, W. 1983. Characterization of lupine proteins. *Journal of Food Science* 48: 38–41.

Palmer, C., Price, O. and Bach, C. 2000. Foraging ecology of the black flying fox (*Pteropus alecto*) in the seasonal tropics of the Northern Territory, Australia. *Wildlife Research* 27: 169–178.

Palmer, C. and Woinarski, J.C.Z. 1999. Seasonal roosts and foraging movements of the black flying fox (*Pteropus alecto*) in the Northern Territory: resource tracking in a landscape mosaic. *Wildlife Research* 26: 823–838.

Pizo, M.A. and Oliveira, P.S. 2001. Size and lipid content of nonmyrmecochorous diaspores: effects on the interaction with litter-foraging ants in the Atlantic rain forest of Brazil. *Plant Ecology* 157: 37–52.

Price, O. 1998. Conservation of frugivorous birds and monsoon rainforest patches in the Northern Territory. Unpublished PhD thesis, Australian National University: Canberra.

Price, O.F. 2004. Indirect evidence that frugivorous birds track fluctuating fruit resources among rainforest patches in the Northern Territory, Australia. *Austral Ecology* 29: 137–144.

Price, O.F., Woinarski, J.C.Z. and Robinson, D. 1999. Very large area requirements for frugivorous birds in monsoon rainforests of the Northern Territory, Australia. *Biological Conservation* 91: 169–180.

Prinzinger, R. and Schleucher, E. 1998. Fruits of tall saltbush *Rhagodia eremaea* as an important source of energy and water for arid zone honeyeaters. *Emu* 98: 236–240.

Russell-Smith, J. 1991. Classification, species richness, and environmental relations of monsoon rain forest in northern Australia. *Journal of Vegetation Science* 2: 259–278.

Russell-Smith, J. and Dunlop, C.R. 1987. The status of monsoon vine forests in the Northern Territory: a perspective. Pp. 227–288. In: Werren, G. and Kershaw, P. (eds) *The rainforest legacy. Volume 1.* Australian Government Publishing Service: Canberra.

Russell-Smith, J. and Lee, A.H. 1992. Plant populations and monsoon rain forest in the Northern Territory, Australia. *Biotropica* 24: 471–487.

Russo, S.E. 2003. Responses of dispersal agents to tree and fruit traits in *Virola calophylla* (Myristicaceae): implications for selection. *Oecologia* 136: 80–87.

Schaefer, H.M., Schmidt, V. and Bairlein, F. 2003. Discrimination abilities for nutrients: which difference matters for choosy birds and why? *Animal Behaviour* 65: 531–541.

Shapcott, A. 1998. The pattern of genetic diversity in *Carpentaria acuminata* (Areceae), and rainforest history in northern Australia. *Molecular Ecology* 7: 833–847.

Shapcott, A. 1999. Vagility and the monsoon rain forest archipelago of northern Australia: patterns of genetic diversity in *Syzygium nervosum* (Myrtaceae). *Biotropica* 31: 579–590.

Shapcott, A. 2000. Conservation and genetics in the fragmented monsoon rainforest in the Northern Territory, Australia: a case study of three frugivore-dispersed species. *Australian Journal of Botany* 48: 397–407.

Snow, D.W. 1971. Evolutionary aspects of fruit-eating by birds. *Ibis* 113: 194–202.

Stapanian, M.A. 1982. Evolution of fruiting strategies among fleshy-fruited plant species of Eastern Kansas. *Ecology* 63: 1422–1431.

StatSoft Inc. 1984–2004. *Statistica 7.* StatSoft Inc.: Tulsa.

van der Pijl, L. 1982. *Principles of dispersal in higher plants.* Springer-Verlag: Berlin.

Webb, L.J. and Tracey, J.G. 1981. Australian rainforests: patterns and change. Pp. 605–694. In: Keast, A. (ed.) *Ecological Biogeography of Australia.* Dr. W. Junk: The Hague.

Wheelwright, N.T. 1993. Fruit size in a tropical tree species: variation, preference by birds, and heritability. *Vegetatio* 107/108: 163–174.

Willson, M.F., Irvine, A.K. and Walsh, N.G. 1989. Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographic comparisons. *Biotropica* 21: 133–147.

Willson, M.F. and Whelan, C.J. 1990. The evolution of fruit color in fleshy-fruited plants. *The American Naturalist* 136: 790–809.

Woinarski, J.C.Z. 1993. A cut-and-paste community: birds of monsoon rainforests in Kakadu National Park, Northern Territory. *Emu* 93: 100–120.

Woinarski, J.C.Z., Tidemann, S.C. and Kerin, S. 1988. Birds in a tropical mosaic: the distribution of bird species in relation to vegetation patterns. *Australian Wildlife Research* 15: 171–196.